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The neuroethology of spontaneous mimicry and emotional contagion in human and non-human animals

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Highlights

- Yawn contagion and play face mimicry are found in human and non-human animals
- In humans facial muscle contraction has a causal effect on brain emotion generation
- Mimicry phenomena highlight a correlative link between bodily and emotional states
- This link, found in animals, may be evolutionarily more ancient than expected
- A shared approach is proposed for research on human and non-human animals

Abstract

Spontaneous mimicry appears fundamental to emotional perception and contagion, especially when it involves facial emotional expressions. Here we cover recent evidence on spontaneous mimicry from ethology, psychology and neuroscience, in non-human and human animals. We first consider how mimicry unfolds in non-human animals (particularly primates) and how it relates to emotional contagion. We focus on two forms of mimicry-related phenomena: facial mimicry and yawn contagion, which are largely conserved across mammals and useful to draw evolutionary scenarios. Next, we expand on the psychological evidence from humans that bears on current theoretical debates and also informs non-human animal research. Finally, we cover the neural bases of facial mimicry and yawn contagion. We move beyond the perception/expression/experience trichotomy and from the correlational to the causal evidence that links facial mimicry to emotional contagion by presenting evidence from neuroimaging, direct manipulation, neuro-stimulation and lesion studies. In conclusion, this review proposes a bottom-up, multidisciplinary approach to the study of spontaneous mimicry that accounts for the evolutionary continuity linking non-human and human animals.

Keywords: spontaneous mimicry, emotional resonance, yawn contagion, play face, primates

1. Introduction

What are the building blocks of social and emotional interaction? What basic mechanisms underpin phenomena such as emotional contagion? These questions concern scientists in biology, psychology and the intersecting field of neuroscience. Contrasting views about the same topics are often proposed, partly because such phenomena are investigated separately in non-human animals (frequently by biologists) and humans (usually by psychologists). This situation fuels the debated divide between non-human and human cognitive abilities, rather than posing emphasis on the shared abilities of non-human and human animals (e.g MacLean, 2016). While working with different theoretical frameworks and methodological tools in these domains, we believe that a fruitful avenue for interdisciplinary convergence is the exploration of spontaneous mimicry, in which the observer automatically matches the perceived motor behaviour (Preston and de Waal, 2002; Drimalla et al., 2019). This behaviour can be a gateway to emotional perception and transmission from one individual to another (emotional contagion, better described below; de Waal and Preston, 2017), especially when mimicry involves facial expressions. In this review, we present a bottom-up (*sensu* de Waal and Ferrari, 2010), multidisciplinary approach to the study of spontaneous mimicry. This approach does not consider humans as a separate pinnacle of animal evolution. It accounts, instead, for the evolutionary continuity linking non-human and human animals (Darwin, 1859) and that overarches ethology, psychology and neuroscience.

Our review starts with non-human animals, especially non-human primates. We discuss how studying the replication of facial displays by social partners offers a behavioural window on

emotional synchronization and contagion. We specifically focus on yawning and play face, two plesiomorphic forms of facial displays, as they are present in phylogenetically distant groups of mammals and therefore particularly appropriate to draw evolutionary scenarios (e.g. Baenninger, 1987; Campbell and de Waal, 2011; Campbell and de Waal, 2014; Davila-Ross et al., 2011; Demuru and Palagi, 2012; Norscia and Palagi, 2011; Palagi et al., 2009; Palagi et al., 2018a; Palagi et al, 2019; Romero et al., 2013; de Waal and Preston, 2017). In this part, we first provide evidence of the presence of facial mimicry and yawn contagion in non-human animals (e.g. de Waal and Preston, 2017) and then we discuss the possible relation of such behaviour with emotional contagion, also addressing (and trying to reconcile) the debate between attentional-based versus affiliation-based accounts for the social modulation of yawn contagion (e.g. Gallup and Massen, 2017; Norscia and Palagi, 2011; Norscia et al, 2016a).

Later, we expand to aspects regarding spontaneous mimicry that are actively investigated in the human literature, and could in part also apply to non-human animal research, such as the possible role of mimicry in emotion understanding and its modification by social relationships (Duffy and Chartrand, 2015; Hess and Fisher, 2013; Kavanagh and Winkielman, 2016; Seibt et al., 2015). In both non-human and human animal research, we discuss proposals that emphasize a process of direct motor matching between the effectors perceived and those activated by the observer (motor resonance). We also discuss an account according to which mimicry unfolds because the detection of an affectively-loaded expression induces in the observer the corresponding emotional state. Research on humans offers evidence that is consistent with the simple direct matching process as well as more complex (i.e. affect-based) simulation processes (Arnold and Winkielman, 2019). Supporting the direct matching view, some studies of facial and gestural mimicry report rapid matching to stimuli that are brief and impoverished (e.g., subliminal, schematic, or robot faces). This matching sometimes occurs in a way that is insensitive to social context (e.g., social relationships), to the perceiver's goals (e.g., matching the opponent's gestures), and is highly dependent on the individual's learning history pairing perception and action (Heyes, 2011).

However, other psychological studies report that some rapid responses are socially modulated. In animals, this is reflected in the high dependency of mimicry on affiliative relations. In humans, this is additionally reflected in phenomena such as rapid counter-mimicry to opponents and reduction of mimicry to out-groups (e.g., Bourgeois and Hess, 2008: Carr et al., 2014, Bagnis et al., 2019).

In the last part of this review, we highlight neuroscientific research from animal and human literature that elucidates mechanisms underlying different forms of mimicry. In particular, we cover the neural bases of facial and autonomic mimicry and yawn contagion (i.e. Dimberg et al., 1982, 1998; Lee et al., 2006;2008; Carr et al., 2003; di Pellegrino et al., 1992; Prochazkova and Kret, 2017; Feldman et al., 2012; Harrison et al., 2006). Based on neuroimaging evidence, we go beyond the perception/expression/experience trichotomy (i.e. Gallese et al., 2004; Iacoboni and Dapretto, 2006; Caruana et al., 2015; Krolak-Salmon et al., 2003). Finally, we move from the correlational to the causal evidence that links facial mimicry to emotional contagion by presenting evidence from direct manipulation, neuro-stimulation and lesion studies to conclude that emotional contagion may, under certain conditions, underlie facial mimicry and yawn contagion, although further explanations remain open (i.e. Hennenlotter et al., 2009; Adolphs et al., 2003; Caruana et al., 2015; Di Cesare et al., 2018).

2. Facial display replication as a behavioural window on emotional contagion

Spontaneous mimicry is the automatic reproduction of the motor patterns (motor mimicry) or physiological state (autonomic mimicry) of another individual and is one of the portals that allows the transmission of emotions from one individual to another, especially when it involves facial behaviour and features revealing internal physiological and emotional states (Kavanagh and Winkielman, 2016; Prochazkova and Kret, 2017; de Waal and Preston, 2017). In this section we first examine whether, and in what forms, the phenomenon of replication of facial displays (play face and yawn) in non-human animals is present and, subsequently, we explore in what cases the replication of facial displays (facial mimicry of play face and yawn contagion) can indicate

emotional contagion as underlying mechanism. While examining these issues, we also present homologies and links with human animals (hereafter: humans) to build the ground for a comparative approach allowing evolutionary inferences.

From an evolutionary perspective, emotional contagion may have arisen in a step-wise fashion, building on the mechanisms that underlie the expression of emotions (Figure 1). The starting point might have been the concurrent or quasi-concurrent expression of the same facial displays by different individuals because of similar physiological responses related to group living (e.g. fear due to predation or aggression; pain due to pathogens or wounds; emotional arousal due to resources becoming available) (Figure 1a). Two further steps may have occurred during evolution (Figure 1b and 1c). The first step is the development of a recognition system in which the facial display of an individual starts working as a *releasing stimulus* (*sensu* Tinbergen and Perdeck, 1951). The *releasing stimulus* elicits the same facial display in other individuals, possibly optimizing the synchronization of their activities (e.g., spatial ranging, coordinated foraging, and sleep/wake rhythms) and therefore has been likely favoured by natural selection. At an automatic level, this process implicates the activation of common neural substrates for the observed and executed action leading to the output of the observed action (Hecht et al., 2013). As a second step, this *motor* contagion might have served as a exaptation for *emotional* contagion when involving displays of emotional internal states, such as facial expressions (Hess and Fischer, 2013).

During evolution, motor mimicry (Figure 1b) and emotional contagion (Figure 1c) may have not necessarily emerged one after another (motor mimicry before, emotional contagion later). Because of the strong benefits of emotional transfer within social groups and possible strong positive selective pressure, motor mimicry and emotional contagion may have been coopted and may have concurrently emerged as a result of the mutual positive feedbacks exerted one over the other.

2.1. Facial displays as releasing stimuli: from individual to social responses

As mentioned, the simultaneous expression of the same facial display by different individuals of a social group, generated by similar physiological internal states in response to the same external event, may have acquired a communicative value during evolution. In this process, single and independent displays may have become *releasing stimuli* eliciting similar responses in other subjects. From an empirical perspective, to verify whether the *releasing stimulus* mechanism is in place, it should be demonstrated that it is significantly more likely subjects display a certain facial configuration when they can perceive it on the face of another individual (experimental condition) than when they do not perceive it (baseline condition).

This approach can be used with different types of the replication of facial expressions that can be categorized as a function of differences in response delay and/or type of display performed: rapid facial mimicry (RFM), delayed facial mimicry (DFM), and yawn contagion (YC) (Palagi et al., 2018a; Davila-Ross et al., 2011; Provine, 2005). RFM takes place when the replication of the facial expression occurs within 1 second (in humans: 500ms; Hess and Fischer, 2013) after presentation of the triggering stimulus (Dimberg, 1997; Dimberg and Thunberg, 1998; Sestito et al., 2013). Delayed Facial Mimicry (DFM) usually occurs with a delay of one to five seconds after presentation of the stimulus (Davila-Ross et al., 2011; Palagi et al., 2018a). Yawn contagion occurs when someone yawns in response to another's yawn: this response delay can range from less than 1 s (falling in the range of RFM), 1 to 5 s (falling in the range of DFM) or, more frequently, extends to several minutes, with a peak response within the first 3/3.5 minutes (Palagi et al., 2009; Palagi et al., 2014; Campbell and Cox, 2019). It is therefore under debate whether and to what extent yawn contagion is the expression of other forms of mimicry (Yoon and Tennie, 2010). The different developmental timeline and the varying delays in the replication of the facial display suggest that mimicry is not a unitary phenomenon and may point towards different underlying mechanisms. From the neurobiological point of view, longer delays in the response suggest that more indirect neural pathways can be involved (Ferrari et al., 2009).

2.2 Yawn contagion

Even though spontaneous yawning is considered a fixed action pattern, its description is not fixed at all. Spontaneous yawning has been described as consisting of long, deep inspiration, brief peak with apnea (acme) followed by a *slow* expiration (Walusinski and Deputte, 2004; Guggisberg et al., 2010) sometimes reported as *rapid* (Baenninger, 1997; Krestel et al., 2018) or *shorter* (Provine, 2012; Gallup et al., 2016). When integrating the different descriptions of the motor patterns defining a yawning event (Walusinski and Deputte, 2004; Guggisberg et al., 2010; Provine, 2012; Baenninger, 1997), it is possible to claim that it includes active jaw gaping, eye closure, contraction of facial muscles, and passive jaw closure, accompanied by neck stretching and head tilting and, in some cases, by limb and body stretching. Due to its complicated combination of patterns, Provine (2012) distinguished different types of yawn (close-nose yawn; clenched-teeth yawn; sealed-lips nose yawn; the eyes-open yawns) showing that some features of yawning can be modulated (Krestel et al., 2017). For all these reasons, a yawning pattern includes a facial expression but involves more than just facial muscles.

Once elicited, yawning cannot be completely suppressed. Therefore, it has been also defined as a stereotyped or reflex-like pattern (Lehmann, 1979; Provine, 1986). Barbizet (1958, p.203) defined yawning 'halfway between a reflex and an expressive movement'. Indeed, the morphological variability surrounding the yawning display indicates that this behavioural phenomenon is more articulated than a simple reflex (Massen and Gallup, 2017). However, despite the different morphological variants found in some primate species (e.g. chimpanzees; Vick and Paukner, 2010; geladas: Palagi et al., 2009; macaques: Zannella et al., 2017; humans: Provine, 1986, 2012), the basic yawning pattern is plesiomorphic and well recognizable across species (Baenninger, 1987). This makes yawning an excellent behavioural marker to investigate facial display replication in a comparative perspective.

As a physiological response, yawning can be influenced by internal and external factors (e.g. time of the day: Giganti and Zilli, 2011; intracranial/brain temperature; Gallup and Eldakar, 2013).

Yawning is also socially modulated: it is more likely to occur in real social settings, as a result of yawn contagion (Provine, 1989; 2005). However, in Virtual Reality (VR) trials, the physical presence of a researcher during testing significantly inhibited contagious yawning, even though participants were viewing a virtual environment (and virtual yawns) and were unable to see the researcher (Gallup et al., 2019).

The same factors that affect spontaneous yawning are observed in yawn contagion. Contagious yawning, although socially modulated, remains a physiological response and has been found in several animal species, including humans, and it occurs when individuals respond with a yawn after perceiving a yawning from/in others (Provine, 2005; Norscia and Palagi, 2011; Palagi et al., 2009; Demuru and Palagi, 2012; Campbell and de Waal, 2011; Campbell and de Waal, 2014; Romero et al., 2013).

The phenomenon of yawn contagion seems to rely upon the perception-action mechanism also involving the mirror neuron system (Preston and de Waal, 2002; Gallese et al., 2004). Kapitany and Nielsen (2017) suggested that in *Homo sapiens* the increased occurrence of yawning in social conditions - as compared to solitary - may be due not to contagion but to the social setting itself. However, their study showed that the mere presence of others was *not* sufficient to increase the probability of yawning. Instead, in line with what is expected when contagion is in place, they found that the yawning rates were significantly higher in the social non-blind (individuals could see each other and detect others' yawns) than in the blind condition (individuals could not see each other). In both conditions, the auditory component of yawns was excluded by having the participants listening to Chopin's Complete Nocturnes (Kapitany and Nielsen, 2017).

Yawn contagion has been found in all the hominine species: chimpanzees (*Pan troglodytes*: Anderson et al., 2004; Campbell and de Waal, 2011; Campbell and Cox, 2019), bonobos (*Pan paniscus;* Demuru and Palagi, 2012; Tan et al., 2017; but see: Amici et al, 2014 on a vary small sample size) and humans (*Homo sapiens*: Provine, 1986; 1989). Outside the hominine species but still within the hominid family, two reports failed to find yawn contagion in lowland gorillas

(*Gorilla gorilla*; Amici et al., 2014; on a larger sample including a bachelor and a harem group: Palagi et al., 2019). On the other hand, yawn contagion has been found in two cercopithecid monkey species (geladas, *Theropithecus gelada*: Palagi et al., 2009; Tonkean macaque, *Macaca tonkeana*: Palagi and Norscia, 2019) but not convincingly in others. Specifically, yawn contagion has not been found in the Japanese macaque (*Macaca fuscata*, Norscia and Palagi, 2019) and the situation is unclear for stump-tailed macaques (*Macaca arctoides;* Paukner and Anderson, 2005). Stump-tailed macaques yawned significantly more while watching a yawn video than a control video but also showed more self-directed behaviour like scratching, which in primates is related to anxiety (Paukner and Anderson, 2005). Results from stump-tailed macaques suggests that the yawning response may be also linked to anxiety and not necessarily to contagion. Beyond primates, yawn contagion has been found in wolves (*Canis lupus lupus*; Romero et al., 2014) and domestic dogs (*Canis lupus familiaris*; interspecific yawn contagion; Silva et al., 2012; Romero et al., 2013). In dogs the yawning response was found not associated with stress but only with the perception of a triggering yawn emitted by the owner (Romero et al., 2013). Therefore, it seems that phylogenetic closeness is not, *per se*, predictive of yawn contagion.

2.3 Facial mimicry

In this section we move from yawn contagion, which can be expressed in several different social contexts, to forms of facial replication linked to a specific context. Play fighting (also known as rough-and-tumble play or play wrestling) is a good behavioural model for comparative studies on both Rapid Facial Mimicry (RFM) and Delayed Facial Mimicry (DFM) because play behaviour is widespread across mammals (Pellis and Pellis, 2017). Moreover, play sessions are punctuated by a facial expression that is highly specific to the playful context, the relaxed open mouth (ROM) or play face (meerkats, *Suricata suricatta*: Palagi et al., 2019a; various lemur species: Norscia and Palagi, 2016; Palagi et al., 2014; *Macaca spp*: Preuschoft, 1992; Preuschoft and van Hooff, 1995; 1997; Scopa and Palagi, 2016; geladas: Palagi and Mancini, 2011; great apes: Cordoni and Palagi,

2013; Palagi, 2006; 2008; Palagi et al., 2007; Palagi and Cordoni, 2012; Waller and Cherry, 2012). ROM is a signal that may convey the self-rewarding/positive internal state that the subject experiences during play (Bekoff, 2015; Boissy et al., 2007). Different studies indicate the presence of homologies between human and non-human primate ROM. Such homologies include both brain areas responsible for face processing (e.g., *Macaca spp.:* Tsao et al., 2008) and the morphological similarities between the visual component of laughter in humans and play face in non-human primates (Parr and Waller, 2006; Parr et al., 2005; Preuschoft, 1992; Preuschoft and van Hooff, 1995; 1997). The play face and laughter of human and non-human primates (Norscia and Palagi, 2016) are innate (Black, 1984; Davila-Ross et al., 2009) and commonly associated with free play (Panksepp, 2004).

This signal is effective in helping children and non-human animals to manage the playful session (for an extensive review see Palagi et al., 2016). For example, if one playmate uses excessive force or does not follow the reciprocity rules (turn taking, role reversal, self-handicapping), the play fighting session can become unbalanced and lead to real aggression (Fagen, 1981; Palagi et al., 2016; Pellegrini, 2009; Pellis and Pellis, 2017; Pellis et al., 2010). Since playful motor patterns are often 'borrowed' from serious contexts (such as agonistic, anti-predatory, and mating behavior; Bekoff and Byers, 1981; Fagen, 1993; Pellis, 1988; Pellis and Pellis, 2009), ROM is crucial to ensure that the playful mood is communicated from one playmate to the other (Pellis and Pellis, 1996; Pellis and Pellis, 1998). During a playful session the play face emitted by one player can be rapidly mimicked by the playmate.

The short delay typical of RFM led to define it as an automatic, unconscious, or involuntary process (Hess and Fischer, 2013). Considering the importance that RFM may have in social interactions, it has been proposed that this phenomenon is more widespread than previously reported and not confined to humans. In non-human primates, RFM has been found in the great apes (orangutans, *Pongo pygmaeus*, Davila-Ross et al., 2008; chimpanzees and lowland gorillas, Palagi et al., 2018a) and in some monkey species such as geladas (Mancini et al., 2013a) and

Tonkean macaques (Scopa and Palagi, 2016). Outside the primate order, RFM was demonstrated in the domestic dog, which rapidly replicates ROMs of conspecifics while playing (Palagi et al., 2015).

Contrary to RFM, DFM occurs with a larger delay (1 to 5 s). It has been proposed that DFM may be less automatic than RFM (Davila-Ross et al., 2011) and some have suggested that DFM can also allow the expression of the playful mood at a later stage of interaction (Mancini et al., 2013a; Schmidt and Cohn, 2001; Palagi et al, 2018a). In the great apes, for example, DFM was found in chimpanzees but not in lowland gorillas (Palagi et al, 2018a). It is possible that chimpanzees perform DFM to re-affirm their playful intention at a later stage of the interaction, to prolong the positive social contact and favour social cohesion (Palagi et al, 2018a). A further explanation for the presence of the delayed response in chimpanzees (DFM) may be a possible audience effect on response elicitation, with this effect prevailing in chimpanzees due to their higher social cohesion compared to gorillas (Cordoni et al., 2018).

3. From yawn contagion and mimicry to emotional contagion in non-human animals

Unlike other motor patterns, facial expressions can convey information about the internal emotional state of an individual. While some emotional displays may trigger a matching response (e.g., as in the contagion of crying or laughter; Provine, 1992; Jordan and Thomas, 2017), some may not (e.g., anger may elicit fear; Dezecache et al., 2015) at least in humans. The replication of the same facial displays can be one of the behavioural manifestations of the transfer of the *same* emotion from one individual to another (*same face – same emotion* process, Clay et al., 2018). However, in non-human animals the presence of facial mimicry and yawn contagion (same face) is not sufficient, *per se*, to automatically assume that emotional contagion is in place (same emotion). From an operational point of view, it is necessary to demonstrate that the occurrence of facial replication is significantly more likely when emotion or mood sharing is expected to be involved, e.g. between kin and/or individuals that are strongly bonded.

3.1 Proximate factors underlying yawn contagion: emotional or attentional bias?

The relation between yawn contagion and emotional contagion is under debate. While some authors consider yawn contagion as an expression of emotional contagion (de Waal and Preston, 2017), others argue that a visual attentional bias, and not an emotional transfer, can explain why it is more likely that individuals yawn after detecting yawns of others (Gallup and Massen, 2017). These two main arguments can be grouped into two different hypotheses: the *Emotional Bias Hypothesis* and the *Attentional Bias Hypothesis*.

According to the *Emotional Bias Hypothesis* (EBH), the variation of yawn contagion across time and individuals can reflect differences in emotional sharing. In this respect, yawn contagion is biased by the same variables that influence emotional contagion. In humans, yawn contagion increases with age when the ability to identify others' emotions increases and declines in old age when this ability declines (Singer 2006; Bartholomew and Cirulli, 2014; Anderson and Meno 2003; Millen and Anderson 2011; Wiggers and van Lieshout 1985; Saxe et al 2004). Chimpanzees too show a developmental timeline, with an increasing trend in yawn contagion from infancy to adulthood (Madsen and Persson, 2013).

In humans, yawn contagion is also more frequent - and the delay in the response shorter - between individuals sharing strong relationships (family and friends) than between unfamiliar people (Norscia and Palagi, 2011; Norscia et al., 2016a). The relationship between yawn contagion and social bonding is not limited to humans, but also concerns bonobos and chimpanzees. Although social modulation may not affect yawn contagion frequency in immature chimpanzees (Madsen and Persson, 2013), adult chimpanzees yawn more in response to the yawns of in-group compared to out-group members (Campbell and de Waal, 2011). Bonobos can show comparable levels of yawn contagion when observing the yawns coming from group members or stranger conspecifics on video (Tan et al, 2017). However, in naturalistic conditions, Demuru and Palagi (2012) found that within group yawn contagion is highest between subjects that exchange more affinitive contacts. A

further study including both humans and bonobos found that the frequency of yawn contagion was affected by the quality of the relationship between individuals more than by the species, which highlights the importance of social bond in the modulation of yawn contagion (Palagi et al., 2014).

The differences in yawn contagion levels between ingroup and outgroup members in the two *Pan* species are in line with the fact that bonobos are more xenophilic than chimpanzees (Tan and Hare, 2017). In fact, in chimpanzees the differences in yawn contagion are immediately evident when comparing outgroup and ingroup members (Campbell and de Waal 2011), whereas in bonobos differences in yawn contagion are only revealed when considering the relationship quality of individuals of the same group, who can interact socially via affiliation (Demuru and Palagi, 2012; Tan et al, 2017).

Gorillas are phylogenetically very close to the other African hominids, bonobos and chimpanzees (Scally et al., 2012; Stevens et al., 2013), but distant from Old World monkeys, such as geladas. Nevertheless, no yawn contagion has been detected so far in lowland gorillas (Amici et al., 2014; Palagi et al., 2019) whereas in geladas not only was contagious yawning found, but it was also observed that the frequency of yawn contagion correlated with the level of affiliation between individuals and not with their level of spatial proximity. Interestingly, geladas share with gorillas a similar basic social structure (one male unit) but possess higher levels of social affiliation (Dunbar and Dunbar, 1975; Kummer, 1971). In the genus Macaca - whose species can be classified according to different grades of tolerance (from 1 to 4, less to more tolerant; Thierry, 2000) - yawn contagion was not found in the scarcely tolerant Japanese macaques whereas it was detected present in the highly tolerant Tonkean macaques, showing higher and more widespread levels of social affiliation (Palagi and Norscia, 2019). Emotional contagion via facial display replication could have been positively selected during evolution because it helps promoting affective and behavioural synchronization within social groups (de Waal and Preston, 2017; Couzin, 2007). When the aggregation of individuals is the result of spatial more than social closeness (as it is the case of adult gorilla females aggregated around the silverback) or is characterised by high social

canalisation (as it is the case of Japanese macaques compared to Tonkean macaques) the selective pressure over the mechanisms promoting behavioural and emotional pairing may have weakened.

Further support to the relationship between yawn contagion and emotional contagion comes from the comparison across different species. As a matter of fact, the modulation of yawn contagion varies according to the different distribution of social bonding characterizing the different species. There is increasing evidence that social status can affect the degree of emotional involvement of individuals and their interest in what others may feel (Arnott et al., 2009). In bonobos Demuru and Palagi (2012) found that group members would respond most likely to female, whereas in chimpanzees Massen et al. (2012) found that males mostly yawned in response to males on video, even if the yawning response of chimpanzees could be elicited also by other group mates yawning nearby and not only by the video. In the gelada society, Palagi et al. (2009) found the strongest and most specific matching of yawn types between females. In line with the EBH, in bonobos yawn contagion could be related to the fact that adult females represent the bonding and decisional nucleus of the society (Furuichi, 2011), thus playing a key role in affecting the emotional states of others (Demuru and Palagi, 2012; Furuichi et al., 2012). In chimpanzees, the relationship with males can be the most meaningful to the group members because in this species males are the bonding and decisional nucleus (Gruber and Clay, 2016). In geladas, females form coalitions and long-term relationships, support each other in infant rearing and remain together, possibly because they are more emotionally tuned to one another than male-female pairs (Pallante et al., 2016; 2019; Palagi et al., 2018b).

In humans, a certain degree of difference may be present in yawn contagion between men and women but the issue is still under debate (Chan and Tseng, 2017; Norscia et al., 2016a,b; but see Bartholomew and Cirulli, 2014). The cultural influence in shaping relationship dynamics in the different human societies makes it difficult to disentangle social bonding and gender effects in the distribution of yawn contagion.

According to the *Attentional Bias Hypothesis* (ABH), yawn contagion would be the result of a purely motor response. Accordingly, the variations of yawn contagion rates between individuals would be determined by the varying levels of social attention, rather than indexing different levels of emotional involvement. Hence, the higher levels of contagious yawning could be due to more theextra attention (frequency and/or duration) being paid to individuals that are more relevant to the observer, such as familiar subjects, as it occurs in humans and geladas, or dominants, as it occurs in chimpanzees or bonobos (Yoon and Tessie, 2010; Massen et al., 2012; Massen and Gallup, 2017). As recently pointed out (Massen and Gallup, 2017), ABH would be supported by the existing evidence on the different visual detection and perceptive encoding of faces of familiar/in-group subjects compared to unfamiliar ones in humans (e.g., Ganel and Goshen-Gottstein, 2004; Michel et al., 2006; Buttle and Raymond, 2003; Jackson and Raymond, 2006). However, such evidence is not based on yawn contagion case studies, and familiarity or group membership are not defined on the basis of previous social interactions between individuals. In-group members are defined on the basis of their common race (Michel et al., 2006) and individuals are defined as 'familiar' even when they are indirectly known to the study subjects (e.g. a famous person or a person whose image has been shown to the study subjects in a pre-experimental phase; Buttle and Raymond, 2003; Jackson and Raymond, 2006; Ganel and Goshen-Gottstein, 2004). Moreover, patterns of visual attention to faces are also clearly not directional. Kawakami et al. (2014) found that people showed preferential attention towards the eyes when viewing ethnic in-group members but also showed preferential attention towards the nose and the mouth of ethnic out-group members. The same study also found that visual attention did not differ as a function of target race. Michel et al. (2006) tested Caucasian and Asian subjects and found that the participants performed better in the holistic recognition of same-race faces but also that the Asian participants who had been living for about a year among Caucasians were able to perform face holistic recognition regardless of the race. A recent study addressed the issue of attention and familiarity in the context of emotional contagion. Dyads of unacquainted human participants co-viewed emotional movies without interacting directly.

Attention was summoned by the emotional movies that served as triggering event, rather than by the other co-viewing participant. Facial synchrony was linked to the movies events. Notably, however, synchrony was enhanced in real compared to random dyads, thus demonstrating an additional value of contagion in inter-personal processing, while maintaining attention constant. Also, enhanced synchrony in real dyads was paired with cardiovascular synchrony, subjective emotions, and emotional convergence towards previously unknown others (Golland et al., 2019).

At least two conditions must be verified to conclude that the differences in the individual selective attention toward certain targets, more than other factors, are responsible for yawn contagion variation. These conditions are: i) the presence of an increasing trend of attention from certain categories of individuals (e.g. unfamiliar to familiar) and ii) evidence that selective attention, and not some other mechanisms related to the detection of the releasing stimulus, is the main force that drives the yawning response.

Regarding the first condition, literature shows that, in human and non-human primates, social attention does not follow a unique trend. By using the viewing time measured via eye-tracking and showing unknown faces to the experimental subjects, Méary et al. (2014) found that humans had a strong bias towards own-race faces whereas, in rhesus macaques, novel species faces attracted more attention than same species faces. This study did not address the effect of social bonding on attention patterns. By using the duration of gazing at the screen by the experimental subject, Whitehouse et al. (2016) found that Barbary macaques (*Macaca sylvanus*) were more attentive to scratching videos of known than unknown individuals but also found that within the known individuals, macaques were more attentive to those they were weakly bonded to. Concerning chimpanzees, Campbell and de Waal (2011, 2014) reported that the increasing attention was greater toward out-group than in-group members. Schino and Sciarretta (2016), by using live recorded glance rates to assess social attention, found that mandrills (*Mandrillus sphinx*) looked more at their own kin than at non-kin but also at high-ranking than at low-ranking group mates. Clearly, there is

no single pattern of selective attention. Therefore, the mere observation that social, selective attention exists is not sufficient to undermine EBH in favour of the ABH.

The second condition requires the demonstration that selective attention overrides social bonding in eliciting the yawning response. To address this issue, it is crucial to operationalize and define attention. Because in humans and other primates, neuronal activity is so metabolically demanding, the brain is not able to attend and process all incoming sensory stimuli that are present in the environment (Lennie, 2003). Different taxonomies of attention exists, but a widely agreed distinction indicates the existence of two attentional systems: stimulus-driven, bottom-up (or exogenous) attention; goal-directed, top-down (or endogenous) attention (Posner and Cohen, 1984; MacLean et al., 2009; Kaya and Elhilali, 2014; Katsuki and Constantinidis, 2014). Bottom-up attention is primarily guided by externally driven factors and starts with sensory perception and basic processing of the eliciting stimulus. Top-down attention is a voluntary, sustained process, where a particular object relevant to current behavioural goals is selected internally and focused upon or examined (Katsuki and Constantinidis, 2014). Bottom-up and top-down attention may operate independently (Pinto et al., 2013) or in a more or less interactive way, depending on the time scale and the number and variety of environmental stimuli (MacLean et al. 2009; Awk et al., 2012). Bottom-up information can be subjected to sensory gating (filtering out irrelevant stimuli) at the encoding (input) stage and provides first identification clues to be used to selectively attend to goal-relevant information at a later stage (Jones et al., 2016). The two systems share only part of the neural apparatus (the frontoparietal network) and different processes mediate the guidance of attention based on bottom-up and top-down factors (Katsuki and Constantinidis, 2014). The attention that is required to perceive a stimulus does not have to rely on a voluntary mechanism because attention can be involved in pre-attentive processing of the stimulus, to be elaborated via bottom-up or top-down systems at a later stage (Bachman, 2011).

We postulate that bottom-up processes more than top-down selective attention are at the basis of the yawning response because contagious yawning occurs when yawning is triggered

involuntarily in a subject when they perceive another person's yawn (Brown et al., 2017). It is true that the yawning response (or any response) to a releasing stimulus can be elicited only if the stimulus is detected by the potential responder, but the social factor is important. For example, the rates of yawn contagion in kids with autism spectrum disorder are influenced by the familiarity of the target stimulus besides instructions that encourage eye gaze to target (Usui et al., 2013; Helt et al., 2019). Mariscal et al. (2019) found that yawn contagion in ASD children was positively correlated to the blood concentration of oxytocin, the hormone involved in parental and social attachment (Decety et al., 2016). In nonclinical human subjects, Chan and Tseng (2017) found that the perceptual detection sensitivity to yawning expression (the ability to detect a yawn as such) was related to the duration of gaze to the eyes of the stimulus releasing face, but the authors failed to find evidence that eye-gaze patterns modulated contagious yawning.

By using electroencephalographic (EEG) and electrooculographic (EOG) measurements of eye movements and blinks, van Hooff et al. (2010) found that both men and women paid maximum attention (measured via event-related potential, ERP) to both attractive and unattractive opposite sex faces. However, only in males the peak point of maximum attention was followed by an increased attention for the attractive faces. The authors pointed out that this finding is consistent with sexual strategy theory suggesting that men and women have evolved different mating strategies with men being more attentive to attractive faces. Selective attention and related response variation, for the same individuals, depend on the circumstances (e.g. sexual context, threat).

Another element that does not totally fit with ABH is that yawn contagion in humans appears not to be sensitive to the amount of yawn stimuli (Norscia and Palagi, 2011), the sensory cue (auditory, visual or audio-visual) (Arnott et al., 2009; Norscia and Palagi, 2011) or the visual perspective of the triggering stimulus (yawns in orientations of 90°, 180°, and 270° can elicit yawning responses as upright, 0° yawns; Provine, 1989, 1996). In chimpanzees, Campbell et al. (2009) looked across individuals and found no correlations between attention and yawn contagion. Furthermore, Campbell and de Waal (2011) found that the yawning rates of chimpanzees were

higher in response to the yawns of in-group than out-group mates, even though the responding subjects looked longer at out-group chimpanzee videos. Additionally, by testing the yawn contagion levels in chimpanzees across 5 stimuli (i.e. ingroup and outgroup chimpanzees, familiar and unfamiliar humans, unfamiliar species, the gelada), Campbell and de Waal (2014) concluded that chimpanzees do not need to know each yawning individual to show contagion, but the individuals do need to belong to a species with which the chimpanzees have a history of positive social interactions.

In the most recent study on captive lowland gorillas (Palagi et al, 2019) the authors made sure that the yawning stimulus fell into the stereoscopic visual range of the potential gorilla responders while collecting data in the naturalistic setting and controlled for the time that the subject actually looked at the video stimulus in the experimental setting. Despite this control, yawn contagion was not observed.

There is another reason why we expect that contagious yawning and selective attention may not always be correlated. In humans, physical and mental fatigue can induce yawning via cortisol mediated response (Fleming and Pollak, 2005; Thompson, 2014; Thompson, 2017; Thompson and Bishop, 2012). However, literature indicates that stress and mental fatigue result in a reduction of top-down, selective attention, leaving subjects performing in a more stimulus-driven fashion (Boksem et al., 2005; Faber et al., 2012; Joyce et al., 2016). These findings suggest that the perception of the (possibly irrelevant) stimulus via bottom-up attention, favoured in case of fatigue, and not selective attention, is responsible for triggering yawning.

ABH and EBH might not be mutually exclusive and, in certain cases, not easy to disentangle. In children, eye contact is associated with lower level of prenatal testosterone (reduced masculinisation) and may be linked to greater sensitivity to other psychological states and empathy (Knickmeyer et al., 2006; Lutchmaya et al., 2002; Phillips et al., 1992). Krupenye et al. (2017) argued that bonobos may be better empathizers than chimpanzees also based on the greater sensitivity to eye contact and gaze of bonobos compared to chimpanzees. Hence, eye contact may

be related to the expression of empathy but more in the cognitive domain than in relation to pure emotional involvement.

Based on existing evidence, attention could play a role in eliciting the automatic yawning response as a *reactive* process to releasing stimuli when it ensures stimulus detection. However, non-conscious processing and bottom-up (stimulus driven) attention more than top-down, selective attention (*sensu* Bachman, 2011; Katsuki and Constantinidis, 2014; Kaya and Elhilali, 2014) is likely to be involved in yawn contagion. Although ABH cannot be totally discarded at the moment, the strong matching between yawn contagion and emotional contagion biases provide solid support to the EBH (de Waal and Preston, 2017).

3.2 Rapid Facial Mimicry and emotional contagion

When two animals play together, they are completely involved in the action and often engage in dyadic joint attention or mutual eye-gaze, which is generally considered one of the earliest and most salient types of automatic mimicry in humans (Prochazkova and Kret, 2017). The mimicry of playful facial expressions occurs after a few milliseconds since animals have engaged in instantaneous mutual eye-gazing (Scopa and Palagi, 2017; Palagi et al., 2015; 2018a; 2019b). Thus, contrary to yawn contagion, it is difficult to claim that an attentional bias generated by looking some individuals more or for a longer period than others can involve, by definition, Rapid Facial Mimicry.

RFM and emotional contagion are distinct concepts because they do not always overlap (Nakahashi and Ohtsuki, 2015). However, evidence is accumulating that many forms of emotional contagion are mediated by RFM. Compared to the simple presence of non-replicated play face (signal), RFM is more effective in prolonging the playful session in several animal species (Tonkean macaques, Scopa and Palagi, 2016; geladas, Mancini et al., 2013b; chimpanzees and lowland gorillas, Palagi et al., 2018a; dogs, Palagi et al., 2015; meerkats, Palagi et al., 2019a). Contrary to RFM, DFM is not effective in prolonging the session at least in the species in which the

issue has been explored (geladas, Mancini et al., 2013b; Tonkean macaques, Scopa and Palagi, 2016). The mirror response and the short reaction time convey the information that the stimulus has been detected and accurately interpreted thus permitting not only a motor but also an emotional matching of the players that prolong their interactions. Prompt facial matching facilitates an immediate and precise mood sharing, which is at the basis of a perfect coordination between the interactants.

Another important factor, which suggests that facial mimicry is one of the vehicles of emotional exchange, is its social modulation. As it occurs with yawn contagion, there is increasing evidence that subjects who share strong social bonds are also more prone to respond each other through RFM (Preston and de Waal, 2002). In geladas, for example, the peculiar relationship between the mother and her infant translates not only into their high levels of RFM but also into the exceptionally short time of reaction compared to other dyads (Mancini et al., 2013a). In humans, facial mimicry between mothers and infants (i.e. smile replication) is considered a spontaneous positive feedback mechanism that is pivotal in enhancing the emotional connection between the mother and her baby (Murray et al. 2016). Later in ontogeny, the same mechanism originated within the mother-infant dyad will extend to other group members. In chimpanzees and juvenile lowland gorillas, RFM is more frequent between strongly bonded subjects (Palagi et al., 2018a). It is difficult to assess the distribution of RFM in adult gorillas because play is not retained in adulthood (Cordoni et al., 2018).

A recent study on domestic dogs showed that their social bond predicted the frequency of RFM during intraspecific free play. In particular, the RFM rates were highest in response to strongly bonded individuals (dogs living together or interacting at least three times per week), then acquaintances (dogs interacting no more than twice a month) and lastly strangers (dogs that have never interacted before) (Palagi et al., 2015). It seems that also in domestic dogs, rapid mimicry is based on a ‘motor’ and an ‘affective’ identification (Dezecache et al., 2015; Hatfield et al., 1994; Gallese et al., 2004). This is supported by the fact that dogs seem to be more able to catch the

emotional meaning conveyed by specific facial expressions when they come from familiar faces (Muller et al., 2015; Albuquerque et al., 2016).

When deriving from emotional bonds built upon direct social interactions, familiarity between individuals seems to be a good predictor of RFM in human and non-human animals. In this respect, RFM shows the same trend of emotional contagion. One major issue under discussion is whether mimicry is an expression of emotional contagion as a precursor to a more general mind-reading capacity or if it is the expression of more sophisticated forms of emotional processing, such as cognitive empathy, which requires that an individual understands the emotion expressed by another individual (Prochazkova and Kret, 2017). Regarding facial display replication, the framework presented above shows that this issue may rise from the fact that different forms of mimicry, rapid and delayed, and contagion are not a unitary phenomenon and probably recruit different mechanisms related to different levels of automaticity. In particular, it is possible to draw a predictive model of response delays in yawn contagion and mimicry based on cognitive engagement and emotional bonding. The delay in the yawning response to others' yawns is not expected to be related to cognitive engagement whereas the level of emotional bonding between individuals (informed by the social bonding) can reduce the yawning response delay (Figure 2a). The delay in facial mimicry response is expected to decrease as the level of familiarity between individuals (informing emotional bonding) increases. On the other hand, the mimicry delay is expected to increases as the level of response automaticity decreases, due to the higher level of cognitive engagement in the mimicry process (Figure 2b). Compared to rapid mimicry, delayed mimicry possibly involves more cognitive resources, which require time to engage. Further investigation is necessary to fully validate this model.

4. Psychological perspectives on mimicry from research on humans

The previous sections focused on two motor patterns - play face (or relaxed open mouth display) and yawning – that are used by different taxonomic groups of social mammals (e.g., play face;

carnivores, including Canidae, Ursidae, Herpestidae: Fox, 1970; Henry and Herrero, 1974; Taylor et al., 2019; primates from strepsirrhines to apes: Norscia and Palagi, 2016; Palagi et al., 2019b). Focusing on those patterns allows cross species comparison in an evolutionary perspective. The previous section particularly addresses the replication of such patterns (play face facial mimicry and yawn contagion) and its possible relationship with emotional contagion, as informed by the literature on non-human animals. In this section, we address recent theoretical developments and empirical discoveries in the literature on humans, especially on facial mimicry, adopting a perspective of continuity with non-human animals (bottom-up approach; de Waal and Ferrari, 2010). Specifically, we will first discuss recent developments in theoretical frameworks guiding psychological research on mimicry. We will consider perception-action, and appraisal frameworks, but we will especially highlight the idea of embodiment – or the notion that perception, experience, and understanding draw on (as in recruit, re-enact with, rely on, and reuse) the perceiver's somatosensory and motor resources. Then we discuss the questions regarding (i) the role of mimicry in emotion detection, recognition and response, and (ii) contextual and social modulation of spontaneous mimicry. Whenever possible, we will relate this discussion back to the models in the non-human animal literature, though the bridge is not yet fully aligned and far from complete.

4.1 Theoretical perspectives

The three broad theoretical frameworks guiding psychological research on mimicry are (i) perception-action theories (Chartrand and Bargh, 1999; Heyes, 2011; Preston and de Waal, 2002; de Waal and Preston, 2017), (ii) embodiment theories (Niedenthal et al., 2005; Schubert and Semin, 2009; Winkielman et al., 2015), and (iii) social appraisal theories (Hess and Fisher, 2013; Manstead and Fisher, 2001). Both the perception-action theories and the early version of embodiment theories (elaborated later) focus on the role of Hebbian associations linking sensory inputs (e.g., seeing a smile) and motor programs (e.g. making a smile). This simple idea explains automatic, spontaneous action to a mere observation of a stimulus (quick smiling to a smile), as well as

vicarious somatosensory phenomena (e.g., we see an object touch our skin and feel a tactile sensation on our skin). The perception-action frameworks seem to best account for the phenomena of rapid, spontaneous facial mimicry (e.g., quick matching of relaxed open mouth display), or mimicry that is slower, yet still shows features of "reflexive" behaviour, like yawning. As pointed out by Heyes (2001), perception-action learning can also explain some basic forms of social modulation. After all, learning is frequency dependent, so that perception-action links are more easily established if we encounter, pay attention, and react to an individual more often. Those links are also more easily activated in contexts that resemble original learning.

In contrast, the social appraisal theories typically see actions as generated from evaluations (appraisals) of stimulus meaning (Scherer, 2009) and interaction goals (Hess and Fisher, 2013). For example, a smile to a smile reflects the perceiver's congruent assessment with others that the situation is positive, and the emergence of congruent positive emotion. Some of the appraisals may be simple, fast and automatic, whereas others are complex, slower and more deliberative (Scherer, 2009). As such, appraisal frameworks can naturally accommodate the distinction between spontaneous, fast, automatic vs. delayed, slow, deliberate mimicry. According to these frameworks, mimicry occurring at later stages and under deliberate control should be subject to more sophisticated modification, though quite complex social modulation phenomena have been observed with rapid and spontaneous mimicry, as we will review below.

Though often presented as competitive, the Perception-Action and Appraisal Frameworks can be potentially reconciled. In fact, as we discuss next, recent versions of social embodiment theories incorporate the role of social context and social goals (as highlighted by social appraisal theory) as parameters that control the extent and form of embodiment. More specifically, several researchers have recently highlighted that all embodiment processes, from action (including mimicry) to language, are sensitive to context and goals (Barsalou, 2017; Borghi, 2018; Zwaan, 2014). In some way, these revisions bring cognitive embodiment theories closer in line with neural frameworks that have emphasized the interaction of goals with sensorimotor processing in

perceiving and understanding actions (Keyser and Gazzaniga, 2009). One recent formulation in the domain of emotion and social cognition, which is particularly suited for discussing mimicry, has been proposed by Winkielman and colleagues (Winkielman et al., 2018). For the current purposes, two assumptions are key: i) situational and social context can shape the pattern of motor involvement, ii) the extent of motor involvement depends on inferential goals, and the need for embodied simulation. As we will see shortly, these new assumptions are reasonably supported by empirical research in psychology.

Before we start, however, a few terminological clarifications are useful. One is the distinction between "mimicry" and "embodied simulation." Mimicry is defined as an observable behaviour – matching of motor pattern (visible via external behavioural observations, covert EMG activity, or activation of the brain's motor circuits). Embodied simulation is a putative process by which the perceiver generates motor, sensory, or bodily activity in order to, for example, facilitate information processing and emotion understanding. Note that this is a higher-order psycho-social construct, similar to constructs such as "emotional resonance" and "contagion". This distinction between "mimicry" and "simulation" becomes especially important for discussions of matching phenomena that are fast and spontaneous (unbidden, with features of automaticity). While the functional "why" questions are difficult, these theoretical frameworks organize key debates in psychological literature about whether such spontaneous matching phenomena are due to repeated pairing between perception and action, and whether somatosensory and motor activity has a causal or mainly epiphenomenal status for the purpose of internal understanding, as we discuss next.

4. 2 Spontaneous mimicry, emotion detection and recognition

As discussed, there is a variety of human studies showing that mere observation of a facial expression can lead to spontaneous and quick generation of matching facial movements (Dimberg, 1982). They occur even when participants are asked to inhibit a facial response (Korb et al., 2010) or when they are asked to respond to the perceived facial stimulus in the opposite way ("counter-

mimicry"; Dimberg et al., 2002). As expected with automatic responses, spontaneous facial mimicry occurs after minimal stimulus input, even upon brief presentations for expressions of joy or anger (Bornemann et al., 2012; Dimberg et al., 2000). Interestingly, both motor and affective processes play a role in such spontaneous matching (for more see Moody et al., 2007; Neumann et al., 2014). In fact, the human and non-human animal literatures converge on the importance of recognising that pure motor-based and affect-based mimicry can be two interconnected but not necessarily coinciding phenomena. In fact, recent human evidence shows that performance on tasks tapping into different aspects of non-affective motor-mimicry (automatic finger mimicry vs. spontaneous gesture imitation) can be uncorrelated (Genshow et al., 2017).

More interestingly, the human literature emphasizes an additional function of such matching – its facilitatory role in perception, experience, and understanding. As also discussed in section 5 of this article, preventing participants from engaging expression-relevant facial muscles can impair their ability to detect briefly presented or otherwise ambiguous facial expressions that involve that specific muscle (Bulnes et al., 2019; Davis et al., 2017; Neal & Chartrand, 2011; Niedenthal et al., 2001; Oberman et al., 2007; Stel and Knippenberg, 2008). Studies also show that inhibition of smiles leads to poorer differentiation between "true" and "false" smiles – a process that relies on processing of subtle facial distinctions (Rychlowska et al., 2014). Finally, as discussed more fully later, some studies show that natural lesions and experimental (temporary) inactivation of sensory-motor areas impair emotion recognition (Adolphs et al., 2000; Pitcher et al., 2008). Of course, there are boundary conditions for the role of facial mimicry in emotion recognition. One such condition is subtlety and complexity of emotion judgments. For instance, in one study using simple emotion decoding, observers mimicked emotional faces, but the degree of mimicry was not correlated with decoding accuracy (Blairy et al., 1999). However, when the task is more complex, as in perceiving authenticity of a smile, fEMG activity did predict judgments (Korb et al., 2014). Similarly, Calder et al. (2000a) found that three patients with Mobius syndrome (a congenital condition that causes facial paralysis, thus preventing mimicry) were impaired only at high levels of recognition

difficulty. Some participants may also develop alternative emotion-recognition strategies, relying solely on visual patterns, as suggested by studies on individuals with autism (Rutherford and McIntosh, 2007). On the other hand, a recent study in children around age 6 suggests a reduction in autonomic responsiveness and recognition ability in the Mobius group, compared to age-matched controls (Nicolini et al., 2019). As far as we know, very little work has been done on this potential function of mimicry in non-human animals. However, such a "recognition aid" function should be more pronounced in situations where there is need for perceptual and/or affective understanding. As such, it is unlikely that phenomena such as "yawn contagion" plays that facilitatory function in perception, though studies need to be done.

4.3. Modulation of Spontaneous Mimicry by Social Context

As we discussed, spontaneous mimicry often follows simple, direct-matching rules (e.g., yawn-to-yawn and smile-to-smile). However, similarly to non-human animals, it is also clear that such behaviour can be modulated by the social context in which the interaction occurs. Psychological research shows that spontaneous mimicry is sensitive to social cues such as prosociality (Leighton et al., 2010), group membership (Bourgeois and Hess, 2008; Bagnis et al., 2019), attitudes (Likowski et al., 2008), and competition (Weyers et al., 2009). Thus, the broader social context comprises both individual states and traits that modulate the presence and intensity of spontaneous facial mimicry (for reviews, see Arnold and Winkielman, 2019: Duffy and Chartrand, 2015; Hess and Fischer, 2013; Kavanagh and Winkielman, 2016; Seibt et al., 2015). As discussed in the literature, some of such social modulation can be explained by the role of simple variables such as attention, familiarity, learning context, or general motivation (Heyes, 2011). For example, as discussed earlier, the speed and frequency of yawning is socially modulated by social relationship, but this is probably due to basic attention, memory and affiliative processes.

Interestingly, in humans, there are situations where social relationship not only changes the extent of spontaneous mimicry, but fundamentally reverses its direction – switching from direct

matching (e.g., smile to a smile) to its opposite -- counter-mimicry (e.g., smile to an expression of anger). One example of social modulation in spontaneous mimicry comes from research considering the dominance relationships between individuals. Non-human literature (reported earlier in this review) shows increased levels of mimicry response when emotional expression is emitted by socially relevant individuals (e.g. dominant females in bonobos, dominant males in chimpanzees, etc.; Furuichi et al., 2012; Gruber and Clay, 2016). In humans, earlier work in psychology has noticed a phenomenon called complementarity, where, as opposed to mimicry, the respondent adopts an opposite, yet fitting postural behaviour (Tiedens and Fragale, 2003). This can occur spontaneously – in the sense of a behaviour occurring without explicit intention, external prompting, or clear awareness (Carr and Winkielman, 2014). For example, participants interacting with a target may spontaneously display a submissive posture (postural constriction) or dominance (postural expansion). However, this earlier research did not address the question of rapid facial expressions. Carr et al. (2014) examined this phenomenon in the domain of spontaneous facial mimicry with time-sensitive fEMG measures. They found that responses to a target's face depend on the participants' own power level, the status level of the target, and the emotion of the target's expression. Interestingly, low-power perceivers smiled in response to angry expressions of high power targets – a pattern suggesting complementarity (submission to dominance). Even more interestingly, high-power perceivers also smiled more when other high-status targets expressed anger. This could also reflect complementarity, but also competitive "schadenfreude", as suggested next.

The possibility that rapid facial reactions reflect competitive considerations is suggested by recent work on human reactions to android's emotional expressions of anger and joy. In the initial work, setting the stage for this, Hofree et al. (2014) have shown that under "default condition" humans spontaneously mimic artificial agents' (e.g., a human-like robot – an android) smiles and frowns. Interestingly, chimpanzees replicate the yawn expression emitted by an avatar on video (Campbell et al, 2009). Indeed, analyses using timing, amplitude and synchronization indices

suggest that human's spontaneous mimicry reactions to androids share similar temporal dynamics of the android's expression. More importantly, the new research on androids (Hofree et al., 2018) shows that social cues in the perceiver's environment can easily convert such mimicry responses into counter mimicry. This is particularly interesting because some evidence suggests that matching responses are difficult to inhibit (Brass et al., 2001; Cook et al., 2012; Dimberg et al., 2002), although they can be context sensitive (Tamir et al., 2004). More specifically, Hofree et al. (2018) ran several studies on human rapid facial expressions (measured via fEMG) to androids expressions embedded in social context. In their study, participants played repeated games with the android, where the android was either their teammate (cooperative block), or their opponent (competitive block). Overall, participants responded facially to the expressions of the android, but they did so in a way that expressed their own emotional reactions to the valence of the outcome. That is, participants smiled more when they themselves won, and frowned more when they themselves lost. Critically, though, participants displayed these expressions even when the android's expressions communicating the outcome were incongruent with their own, such as during the competitive block (where android's smile communicated participants' loss, and his frown communicated participants' gain). Interestingly, these facial reactions did not differ in timing or magnitude from those in the cooperative block.

In short, the studies discussed in this section suggest that basic facial reactions, even if spontaneous, can be contextually or socially modulated. This has been previously discussed in the context of work on reduced basic mimicry to outgroups (e.g., Bourgeois and Hess, 2008; Likowski et al., 2008). As previously described, chimpanzees yawn significantly more in response to a yawn emitted by an individual of their own group than to a yawn emitted by outgroup individuals (Campbell and de Waal, 2011). In humans, the current studies suggest that rather than "suppressing" or overshadowing basic mimicry reactions, social context can fundamentally shape or even "reshape" them (as in Carr et al., 2014). Specifically, in a larger social context, human facial behaviours can reflect the meaning behind the observed expression, not just the perceptual features

of the expression itself (e.g., we not only fail to mimic a smile if that expression carries implicit negative consequences, but we actively do the opposite -- frown). In this process, emotional expression seems therefore mediated by elements of emotion understanding, a higher cognitive level compared to just emotional resonance activated by the *same-face-same-emotion* process mentioned in the previous part of this review. More broadly, it now appears clear that context can fundamentally shape even the most basic and rapid reactions to targets. This once again highlights the importance of considering mimicry within social context, reflecting the inherent "intelligence" of the underlying process. Having said that, note that this "intelligence" may sometimes reflect the fact that different contexts simply "call" for different bodily reactions, reflecting evolutionary adaptation of different reactions to different contexts and, more proximally, learning mechanisms sensitive to contextual shaping (Heyes, 2011). Interestingly, in the literature on human behaviour, there is little evidence for such clever modulation of yawning (but see Platek et al., 2003). On the one hand, this could be surprising given that yawning often has a slow dynamics and is susceptible to social modifications (we will return to this issue in section 5). On the other, this may reflect the fact that yawning is basic fixed action pattern whose contagion may be the result of an exaptation mechanism over a plesiomorphic trait (as discussed in section 3).

5. Neural bases of mimicry and emotional contagion

As discussed above, the relationship between replicative processes (e.g., multiple forms of facial or yawn mimicry) and their role in emotional contagion and resonance has come under renewed scrutiny (Massen and Gallup, 2017; Prochazkova and Kret, 2017). As it happens, the current debate primarily focuses on *ultimate explanations* of replicative processes and their evolutionary meaning; i.e., why mimicry takes place and what fitness benefit it provides. On the other hand, *proximate explanations* seek to understand how mimicry occurs, which neural or psychological factors modulate it, whether and how mimicry can give rise to emotional contagion (Dezecache et al., 2015). Proposals envisaging mimicry as a precursor and necessary determinant of emotional

contagion rest on several common assumptions. First, emotion recognition and its expression are not separate neuro-cognitive systems. Second, facial expressions and other mimic reactions (e.g., smiling, yawning), although spontaneous and automatic, serve communicatory functions. Third, emotion recognition and understanding are based on a common simulation mechanism, whereby the attribution of an affective state to others depends on enacting the same state, starting from observable expressive behaviors (Gallese and Caruana, 2016; Goldman and Sripada, 2005; Niedenthal, 2007; Wood et al., 2016). Investigation of the neural bases of mimicry and its breakdown after brain damage provides a valuable testing ground for these assumptions. In fact, neuroscience can address directly proximate explanations, while offering additional insights, albeit indirect, on ultimate explanations concerning the relationship between mimicry, contagion and emotion understanding.

5.1 Neural bases of mimicry and yawn contagion

The idea that facial expression of emotions has a biological basis (Darwin 1872) seems to suggest that facial expressions operate automatically and independently from conscious cognitive processes. The initial response to affective stimuli can be generated without conscious awareness and could be measured because facial expressions elicit facial muscular activity congruent with the presented facial expression (Zajonc, 1980). Dimberg (1982) showed that mere exposure to pictures of angry and happy facial expressions induced spontaneous corrugator supercilii muscle activity and zygomatic major muscle activity respectively. Specifically, Dimberg and colleagues (1998) showed that facial EMG activity occurred after only 500 ms from exposure to the facial picture, thus implying that facial muscle activity occurs spontaneously and rapidly in response to facial expressions. Hatfield et al. (1993) also illustrated the relationship between emotional mimicry and emotional contagion, as automatic mimicry of facial expressions also induce the onlooker to converge emotionally, possibly because of facial feedback mechanisms. More recent works with EMG recording (Lee et al., 2006; 2008; Shilbach et al., 2008; Likowsky et al., 2012; Rymarzyk et

al., 2018) confirm previous data on automatic facial responses to emotional stimuli, although with differences for the emotional content (e.g., sad, fear or happy) or the kind of stimuli (static vs. dynamic) presented.People mimic not only motor expressions, but also autonomic signals. Harrison and colleagues investigated whether observed pupil size modulates our perception of other's emotional expression, showing that pupil size of the onlooker mirrors the observed pupil size of the displayed face in the context of sadness. The results thus lend support to the idea that the perception-action mechanism extends to non-volitional operations of the automatic nervous system (Harrison et al., 2006). They found activity in two symmetric regions within the mid-brain and also in the right angular gyrus. The mid-brain activity encompassed the Edinger-Westphal nuclei responsible of pupil size control. In addition, they found a correlation with areas like left frontal operculum, amygdala and superior temporal sulcus (STS). The role of mutual eye-gaze in automatic mimicry is related to other forms of mimicries (Feldman, 2012; Wang et al., 2011), making of it a likely source of contagion (Kret, 2015; Prochazkova and Kret, 2017).

Since the discovery of mirror neurons, they have been discussed as a likely mechanism for facial mimicry and the convergence of observation and action into a common neural code (Carr et al., 2003). Originally reported in premotor areas of the macaque, mirror neurons respond both when the monkey performs an action and when it looks at the same action being performed by the experimenter (di Pellegrino et al., 1992; Rizzolatti et al., 1996, 2001; Rizzolatti et al., 2002). This mechanism has been described also in humans and encompasses the ventral premotor cortex (vPMC), the inferior frontal gyrus (IFG), the IPL (inferior parietal lobe) and the STS (superior temporal sulcus). Sato and colleagues (2004, 2007) found that, in addition to the temporal cortex, the pars opercularis of the inferior frontal gyrus was more active in response to the dynamic facial expression and facial action than in response to control stimuli. Recent studies, however, reveal a slightly more complex picture. Gazzola and Keyser (2009) examined shared voxels that show increased BOLD activity both during observation and execution of an action (i.e. neuron mirror) in a wide range of areas. Those voxels were located in the classical mirroring regions but also areas

beside the MNS, like dPMC, SMA, MCC, the somatosensory cortex (BA2/3), SPL, MTG, and the cerebellum (Likowski, 2012). Nummenmaa and colleagues (2008) proposed that "emotional mirroring" may be supported by two separate pathways: one that is based purely on physical imitation (similar to a motor imitation) of the observed emotional behaviour, and another that is based on the somatosensory and motor responses triggered by the emotional content of the stimulus.

The literature concerning the neural bases of contagious yawning is scanter and less conclusive. Indeed, because of the scarcity of articles, the different methodologies (EEG, TMS, fMRI) and the variety of experimental designs used to investigate contagious yawning, there is little agreement on which areas are most relevant for this phenomenon. The TMS study by Brown and colleague (2017) reported that the individual propensity to contagious yawning is related to cortical excitability of area M1. The involvement of hMNS is also suggested by the EEG study by Cooper and colleague (2008, 2012). In fact, the authors found greater mu suppression in hMNS network when participants observed pictures of yawning individual than non-yawning control stimuli. Because desynchronization of mu power is considered a putative index of hMNS activation, these results were consistent with the only neuroimaging study that found implications of the hMNS in contagious yawning (Arnott et al. 2009). Nevertheless, fMRI literature provides contrasting findings about the involvement of hMNS in contagious yawning. Several authors (Platek et al., 2005, Schürman et al., 2005; Nahab et al., 2009, 2010) have identified activity in different areas like precuneus, posterior cingulate areas, STS or ventromedial prefrontral cortex, but not in the hMNS related areas. These incongruences can be partly related to the different paradigms used as well as to the choice of different stimuli (Cooper et al., 2012).

As it happens, facial mimicry and yawn contagion seem to share some areas while diverging on others. Areas like vmPFC, STS and amygdala seem to be involved in both phenomena; insula, premotor areas, IFC, IFG are prevalent in the facial mimicking processes while posterior cingulate and precuneus seem to be more related to the yawning contagion. Areas related to attention processes appears more involved in orienting-bottom up network (TPJ, brainstem nuclei, vlPC) than

top-down related areas (FEF, IPS, parietal areas), thus supporting indirectly the emotional bias hypothesis against the top-down, attentional bias hypothesis.

Neuroimaging evidence: beyond the perception/expression/experience trichotomy

Neuroimaging research in social neuroscience indicates that observation of another person's emotional expression activates brain areas overlapping with those involved when the onlooker experiences or displays the same affective state. For example, Wicker and colleagues (Wicker et al., 2003) examined with functional MRI (fMRI) the areas involved during first-person experience of disgust, as induced by inhalation of unpleasant odorants, and during visual observation of facial expressions of disgust. They found that observation and experience of disgust overlaps in the same sectors of the anterior insula and anterior cingulate cortex (ACC). In another classic neuroimaging study, Carr and colleagues (2003) used fMRI while subjects were either imitating or simply observing emotional facial expressions. Imitation and observation activated largely similar areas in a neural network encompassing premotor areas in the inferior frontal cortex and in the superior temporal sulcus (STS), which are both relevant for action understanding. In addition, significant activity was reported in the insula and amygdala, which are constitutive components of emotion processing. Further fMRI studies have similarly shown that passive visual exposure to specific emotional expressions activate in the onlooker the same neural areas involved in the generation of the same emotional expressions and/or affective state, including fear, anxiety, reward, or pain (de Gelder et al., 2004; Hadjikhani et al., 2009; Jackson et al., 2006; Mobbs et al., 2009).

These findings are consistent with an extended model of the MNS to humans and to socio-affective functions (Gallese et al., 2004; Iacoboni and Dapretto, 2006). Accordingly, expressive facial or bodily movements communicating emotions likely represent an instance of a more general mirroring phenomenon. In fact, action mirroring is known to generate cover activation of distal muscles homologous to those engaged in the perceived action (Fadiga et al., 1995). The extended MNS in humans comprises the ventral premotor cortex (vPMC), the inferior frontal gyrus (IFG), the

inferior parietal lobule (IPL) and the superior temporal sulcus (STS). Additional areas are recruited during expression/recognition of specific emotions, such as the amygdala for threat processing and defensive responses (Celeghin et al., 2017; Diano et al., 2017; LeDoux, 1996, 2000), the basal ganglia for anger (Calder et al., 2004), the pregenual sector of the anterior cingulate cortex (pACC) for smiling and happiness (Caruana et al., 2015; Pillay et al., 2007), and the anterior insula for disgust (Krolak-Salmon et al., 2003; Sprengelmeyer et al., 1998; Wicker et al., 2003). Besides its specific role in mediating disgust, the insula is also conceived as a general-purpose relay from action representation in premotor areas to structures encoding emotional value in limbic areas. Building on these and other results, the two separate pathways proposed for mimicking of facial expressions by Nummenmaa and collegues (2008) seems highly possible.

A parallel line of neuroimaging studies focused on the neural underpinnings of yawning contagion and returned somewhat mixed results. Platek and colleagues (2005) reported activation in the posterior cingulate, precuneus, bilateral thalamus and parahippocampal gyrus. While activation in the thalamus, parahippocampal gyrus and STS may be related to processing general sensory components of face perception, activation in posterior cingulate and cuneus/precuneus region has been associated with self-referential processing and retrieval of autobiographical memories (Lou et al., 2004; Maddock et al., 2001). The authors interpreted the data suggesting that contagious yawning involves theory of mind (ToM) or empathy networks. Schürmann and colleagues (2005) displayed videos of yawning people and asked participants to actively resist yawning. They found STS activation, but failed to report significant responses in classic areas hosting mirror neurons, such as inferior frontal cortex, and suggested that highly stereotyped motor patterns, such as those involved in contagious yawning, do not require true imitation and would therefore not activate mirror neurons. Nahab and colleagues (2009) sought to better define the brain regions activated while subjects viewed yawn videos as compared with areas activated while viewing similar non-contagious facial actions. It turned out that the ventromedial prefrontal cortex (vmPFC) was specifically involved in the urge to yawn by contagion. Building on this region's association with

emotional processing of internal and external stimuli, they proposed that the urge to yawn via contagion, unlike other non-contagious facial expressions, does not take place through a process of imitation or mimicry. Rather, the primitive motor program is 'released' by the vmPFC and is carried out through brainstem and subcortical mechanisms.

Lastly, neural mechanisms subserving pupil contagion provide evidence that perception-action mechanisms extend also to non-volitional mimicry recruiting the autonomic nervous system. For example, Harrison and colleagues (Harrison et al., 2006) found that pupil contagion, besides brainstem pupillary control nuclei, also recruits other cortical and subcortical regions implicated in social cognition and Theory of Mind (ToM), such as STS, amygdala, frontal operculum and intraparietal sulcus. Moreover, when pupils of interacting partners synchronously dilate, trust decisions are promoted through the activation of ToM network including the precuneus, the temporo-parietal junction (TPJ), STS, and mPFC (Prochazkova et al., 2018). These and other similar data support the contention that pupil size influences the vicarious understanding of expressed emotions and affords an evolutionary ancient neurophysiological mechanism that is active across the primate lineage to promote affiliation, bonding, and trust through mimicry (Carsten et al., 2018; Kret, 2015; Kret and De Dreu, 2017).

Collectively, neuroimaging studies are compatible with accounts suggesting that basic aspects of mimicry are precursors of, and can give rise to, emotional contagion and, ultimately, to the understanding of other's emotions through overt or covert simulation (Goldman and Sripada, 2005; Prochazkova and Kret, 2017). Clearly, this type of evidence has intrinsic limitations at different practical and conceptual levels. For the present discussion, it is worth mentioning that the correlational nature of the data collected (i.e., a given brain area is associated with a measurable behavior) does not allow inference on the causal relations between phenomena nor on their primacy. Hence, support for the claim that mimicry has a primacy on, and in fact gives rise to, a subsequent emotion state, and that contagions is an integral component of emotion understating in others, should come from different sources of evidence, as reviewed below.

5.2 From correlational to causal evidence: direct manipulation, neuro-stimulation and lesion studies

There is substantial evidence that manipulation and voluntary changes in the contraction of facial musculature has a causal effect in the generation and/or recognition of emotional states and its neurophysiological correlates. As also explained in the psychological section above, intentional manipulation of facial musculature (e.g., asking participants to held a pen between the lips to inhibit smiling vs. held a pen between the teeth to facilitate smiling) causally affects how emotions in others are visually recognized (Adelmann and Zajonc, 1989; Buck, 1980; Han et al., 2016; Niedenthal et al., 2001; Niedenthal, 2007; Oberman et al., 2007; Strack et al., 1988; Zajonc, 1985). Hennenlotter and colleagues (2009), applied botulinum toxin (BTX) to the corrugator supercilii muscle to inhibit angry mimicry while participants viewed emotional faces. The results showed that BTX group exhibited impaired brow lowering and reduced activation of the left amygdala during imitation of angry expression, suggesting a causal influence of facial mimicry on emotional contagion. Neal and Chartrand (2011) extended these previous findings by showing that dampening as well as amplifying facial feedback modulates participants' ability to recognize other people's emotions. In fact, emotion perception was significantly impaired in people who had received BTX compared to control procedures, whereas emotion perception was improved when skin was made resistant to underlying muscle contractions, thereby enhancing facial feedback signals.

If emotion recognition and experience rely on mimicry and expression, then proprioceptive sensations would mediate the matching between these two classes of phenomena. Adolphs and colleagues (2000) found indeed a significant correlation between damage to proprioceptive areas in the somatosensory regions of the parietal cortex and face-based emotion recognition. Likewise, patients with focal lesions to the insula are impaired in both recognition and experience/production of disgust (Calder et al., 2000b; Adolphs et al., 2003). These and other lesion studies in patients with focal brain damage therefore suggest that deficit in the expressive production and/or

experience of an emotion, and impairments in the facial recognition of emotions reliably co-occur (Goldman and Sripada, 2005). Admittedly, it is possible that pairing of deficit in the perception and production of emotions does not result from the functional inter-dependence of the two phenomena, as claimed by simulationist accounts (Goldman and Sripada, 2005), but rather from mere co-localization of perceptual and expressive capacities in the same brain areas. The fact that paired deficits have been reported for distinct emotions, such as disgust, anger or fear, makes the hypothesis of an accidental anatomical overlapping unlikely. Recently, Caruana and coworkers (Caruana, 2017; Caruana et al., 2015, 2018) addressed directly this issue in a series of elegant studies applying intracortical electrical micro-stimulation to patients with pharmacologically resistant epilepsy. Electric stimulation of the anterior cingulate cortex in the pregenual sector (pACC) elicited burst of laugher that, in half of the subjects, was also accompanied by joyful and positive feelings (Caruana et al., 2015). These data challenge the validity of a sharp dichotomy between motor areas (pACC) and areas implementing encoding of emotional signals and associated feelings (temporal cortex) associated with laughing. Likewise, electric stimulation of the amygdala evokes visceromotor responses typical of response to threat that are also accompanied by subjective feeling of fear (Meletti et al., 2006), akin of what observed for anterior insula and disgust (Di Cesare et al., 2018; Isnard et al., 2004; Krolak-Salmon et al., 2003). More broadly, these findings contribute to move our understanding beyond the expression/experience or the perception/expression dualism in emotion research (Gallese and Caruana, 2016) and demonstrate at a micro-scale level that expression/experience overlapping is not simply an epiphenomenon. Rather, evidence that expression and experience of emotions actually map into a common neural code helps situating agency as a core feature of emotional experience and re-joins with early theoretical attempts to uphold the continuity between sensory, motor, and experiential aspects of emotions.

Another source of evidence comes from studies examining neurological patients with damage to different motor centres and the impact on spontaneous versus intentional facial expressions of emotions. A traditional neurological dichotomy separates spontaneous facial

expressions, that are served by the extrapyramidal motor system, of which the basal ganglia are a primary component, from intentional or posed expressions that are mediated by the pyramidal system, which is under cortical control (Rinn, 1984). Although there is partial support for this dissociation, evidence is still scant and results mixed. Patients with Parkinson's disease that affects the basal ganglia present with a reduction in the spontaneous production of affective expressions, as measured in dampened expressive responses to watching emotionally salient movie-clips (Borod et al., 1990; Weddell, 1994; Smith et al., 1996). However, these patients are also impaired in posing facial expressions voluntarily. These results are mirrored by findings gathered from patients with lesions to the cortical motor areas. In such patients, the major deficit is the voluntary facial expression of emotions, with spontaneous expressions relatively preserved (Hopf et al., 1992). However, there are reports of patients with frontal lobe damages that are impaired in the production of both intentional and spontaneous expressions. Therefore, although there is partial support for a double dissociation between voluntary and spontaneous expressions, the nature of the dissociation seems weak and results are partially mixed. The idea of an anatomical difference between "spontaneously-" vs "intentionally-generated" expression system may also be related to the distinction between rapid vs. delayed mimicry. However, relevant research is lacking. Furthermore, one complication is that even some delayed mimicry phenomena (e.g., yawning) show reflex-like features, and some rapid mimicry phenomena (e.g., facial expression) show contextually sensitive modulation (Bagnis et al., 2019). Clearly, further research is needed to understand the neural basis of this distinction.

The relationship between mimicry and emotional contagion has been criticized due to the presence of possible confounding variables such as visual attention or awareness. Neuroscience and experimental psychology are replete with examples of emotion perception occurring without attention and/or visual awareness (Burra et al., 2017; Celeghin et al., 2018; Celeghin et al., 2015; Celeghin et al., 2019; Diano et al., 2017; Negro et al., 2015; Tamietto et al., 2015; Tamietto and de Gelder, 2010). Non-conscious emotion recognition can occur because of either experimental

manipulation that renders the visual stimulus invisible (e.g., backward masking, flash suppression) or as a consequence of brain damage to the visual cortex (blindsight) or the parietal cortex involved in the deployment of spatial attention (e.g., hemispatial neglect or visual extinction). It is worth noting that non-conscious emotion perception is not confined to the sensory system but can also induce spontaneous facial reactions that reflect the affective valence of the stimuli, as recorded using electromyography (EMG) (Dimberg and Petterson, 2000; Dimberg et al., 2000), and pupil dilation (Tamietto et al., 2009; 2015). Therefore, from a different perspective, also these findings speak of an interdependence between perception and production of emotions.

6. Concluding remarks

This review shows that the tools used for investigation in biology, psychology and related neuroscience are complementary and can be joined in an overarching approach allowing the study of mimicry – and its possible relationship with emotional contagion – in a cross-species, comparative perspective. Collectively, the data build upon interdisciplinary evidence from various fields seem to indicate that mimicry may be a precursor and essential component of emotion recognition and contagion. From an evolutionary point of view, it may be a rather ancient phenomenon, which enables an organism to perceive and identify the emotions of others by relying on the same apparatus and machinery that is already used to generate or experience the same emotions. Several questions emerge from the human literature that could be fruitfully addressed by the animal literature. To what extent are the motor components of mimicry necessary for (a) emotion processing, and (b) emotional contagion? Would causal manipulations lead to similar conclusions? What are the conditions under which spontaneous mimicry gets reduced, amplified, or even reversed – turning into complementarity? This review is just an initial attempt to harmonise different disciplinary views on spontaneous mimicry and its possible relation to emotional contagion, but it seems clear that the field is ripe for synchronizing the developments in the psychological and ethological literature on humans with the literature on other animals.

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Figures

Figure 1 – Ethological model for the evolution of emotional contagion. Step 1 – Solitary displays. Individuals independently show similar facial displays in response to a common external releasing stimulus. Simultaneity is the by-product of perceiving the same stimulus at the same time. Step 2 – Social displays. The facial display of a subject acts as releasing stimulus for the other subject. The other replicates the expression as a result of the action-perception mechanism. Step 3 – From motor to emotional contagion. Motor contagion leads to emotional contagion with the replication not just of the motor pattern but also of the internal emotional state.

Figure 2 – Predictive model of response delays in yawn contagion and mimicry trends based on the implication of cognitive abilities and emotional bonding. Both dotted and solid lines do not indicate a linear function but only the increasing/decreasing trend. 2a – The yawning response to others' yawns (contagion) is an automatic, pre-conscious response whose delay is not expected to be related to cognitive levels (dashed lines9. On the other hand, the level of emotional bonding between individuals (informed by the social bonding) can reduce the yawning response delay (solid lines). 2b – The delay in facial mimicry response decreases as the level of familiarity between individuals (informing emotional bonding) increases (solid lines). On the other hand, the delay increases as the level of response automaticity decreases, owing to the higher implication of cognitive processing (dashed lines). This can be applied to Duchenne and Non-Duchenne Laugh in humans and Rapid Facial Mimicry and Delayed Facial Mimicry in chimpanzees.

Fig 1

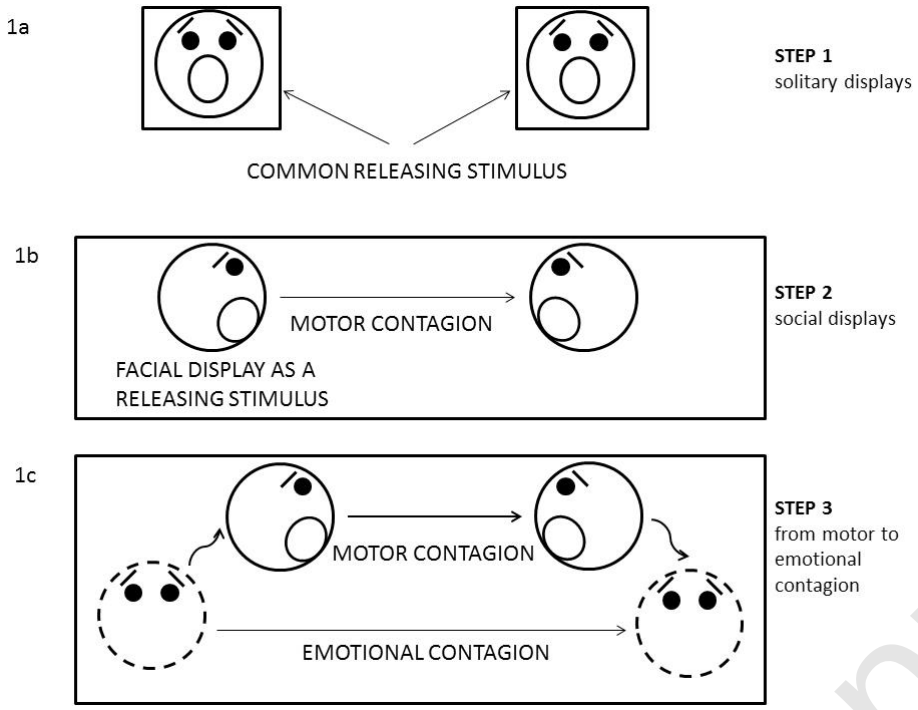

Fig 2